

CHAPTER 1

The Ecology of Terrestrial Fungi

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I. INTRODUCTION

It is widely recognized that in the field of ecology there are fundamental principles that apply to most organisms, including man as well as micro-organisms. Workers investigating a particular type of organism can define processes and formulate principles of application to ecology generally. Conversely work in a restricted field can often benefit from the application of ideas deriving from work on very different organisms. In many ways the ecology of fungi demonstrates these generalities and has great similarities to that of other groups; it has sometimes confirmed work in other fields and sometimes contributed to it. Fungi, because of their small size and their rapid activity permit a study on a smaller scale than do many more traditional ecological materials, and they can be particularly useful in this role. However, partly because fungi have certain special features of somatic morphology, of physiology and of genetics, as described in earlier accounts in these volumes, there are some important ways in which their ecology differs from that of higher plants and animals, and these differences will carry most of the emphasis in this account.

The large surface:volume ratio inherent in the hyphal growth form gives a large contact with the environment and greatly affects fungal biology. Ecologists studying root systems of higher plants have sometimes been impressed with the surface:volume ratio there, but in filamentous, and even more in unicellular, fungi the surface for contact with the environment is extremely high in relation to the total mass of protoplasm. Not only is the area of contact large, but there is no great distance between any point in the protoplasm itself and the environment. Whereas the higher

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multicellular organisms have much of their protoplasm protected from the environment by physical and physiological barriers, in fungi in the somatic condition such barriers are minimal. Except in plectenchymatous structures all the protoplasm is within a few microns of the outside environment, and only a thin cell wall and the plasmalemma separate the two states. For these reasons the environment plays a much more immediate and direct part in fungal behavior than in the behavior of many other organisms. Conversely, the fungus may in turn influence the environment rapidly, and the effect may be large in proportion to the amount of protoplasm present. Where the mycelium is extensive it is as though some of the environment were contained in rather large intercellular spaces of the organism, rather than the organism contained in the environment. Most fungi characteristically have a very rapid and active metabolism, and this also is related to the high surface:volume ratio. The maintenance of life processes in a protoplast involves a disequilibrium between that protoplast and its environment. Normal physical and chemical processes across the boundary act to cancel this disequilibrium, and the larger the boundary the greater the tendency toward equilibrium. The normal disequilibrium of life is maintained across this gradient by the utilization of energy in metabolic activities that hold the protoplasm in a state markedly different from that in the environment. The high rate of metabolism of fungi then is a necessary corollary of their somatic morphology. These relationships also help to explain the rapid and large effects on fungus behavior of apparently small changes in the environment, and further implement the sometimes relatively large effect of the fungus on its environment. Contributing further to these effects is the fact that in the somatic parts of most fungi all cells are metabolizing. In higher plants and animals some cells, often a large proportion, serve a supporting or protecting function and thus reduce the total amount of activity in relation to the total mass of the organism, while, with few exceptions, fungi do not possess such layers of cells that contribute little or nothing to overall metabolic activity. In fungi, in fact, much of cell metabolism occurs much closer to the environment than in higher animals and plants, in which it mostly occurs inside the cells. In fungi much of this activity occurs either outside the cell or just at the cell surface, which may increase the effective area by corrugation or involution. The production by cells of external metabolites or ectocrine substances (Lucas, 1947) is not confined to fungi, but because of the relationships just described such substances produced by fungi have a very obvious importance in their biology. They assist the fungus to exploit its environment even more thoroughly than is possible by surface contact. They also affect the environment, causing alterations and modifications to it, and part of the relevant altered environment may

consist of other living organisms. There is adequate recognition of the importance in microbial ecology of synecological interrelationships. To a great extent these relationships are important because of the facts outlined in this paragraph.

Because an active fungal mycelium metabolizes rapidly and exploits its environment extensively, it is also usual for it to synthesize new protoplasm and to grow in length rapidly. These phenomena assist in the quick colonization of substrata² under suitable external conditions. However, because it is rapidly colonized and exploited, the environment may soon fail any longer to provide suitable conditions for growth of the fungus. There occurs a depletion of nutrients and an accumulation of waste metabolites that can reach toxic concentrations. When the mycelium in any area fails for reasons of this sort to maintain its disequilibrium with its environment, there is a tendency toward a slowing down in the rate of metabolism and toward a loss of organization in the protoplasm. Some fungi have a naturally slower rate of metabolism which avoids rather than counteracts the difficulty. Some fungi actually counteract the deficiency in the environment by a movement of the protoplasm forward within the hyphae, so that there is within the tubular cell wall a migration forward of the active protoplast to regions that permit or favor a higher rate of metabolism. With fungi that do not use this mechanism and that yet inherently need a high metabolic rate for survival, there are two possibilities. Either the metabolic rate slows down involuntarily and the protoplasm soon dies, or the metabolic rate slows down endogenously together with concurrent active and adaptive changes on the part of the fungus whereby physical and physiological barriers are erected between the protoplasm and the environment. These, by limiting the rate of exchange between the two phases, reduce the effects of the equilibrating forces, and allow the protoplast to retain viability without metabolizing much, and without much expenditure of energy and reserves. The change of metabolic condition may be associated with a morphological change. Sometimes swollen and thick-walled chlamydospores are produced, or special asexual structures producing conidia or sporangiospores may result. But similar physiological changes may occur also in superficially normal hyphal segments of one or a few cells, and these can also form a residual viable inoculum of the fungus in regions where it has been active but where most of the mycelium has subsequently died.

Because of the prevalence of study with artificial laboratory culture, it is common to think of fungal colonies as rather large and continuous,

²In this chapter *substratum* is used to designate the material medium in which the fungus occurs, *substrate* to designate the chemical substance acted upon by an enzyme.

but even in such large laboratory colonies it is usual to find that a relatively small proportion of the mycelium, normally the marginal zone only, is metabolically active. In parts of the colony individually older than 1 or 2 days the mycelium has arrived at the stage where somatic activity is at a low level, and usually propagules of some sort, either residual or dispersal, have been produced (Park, 1961). In nature, although fungi may not grow as colonies, a condition similar to this may be normal. Burges (1958) has estimated that some fungal hyphae in soil have a life of 1–3 days at the most. Other types of mycelium with an inherently slower metabolic rate, like that of some basidiomycetes, may of course be longer-lived in soil. However, from the fact that individual hyphal lengths may be very short-lived in nature as in culture it does not necessarily follow that natural death occurs at a high rate in fungi. The protoplasm from the dead hyphae may not itself have died, but may have been transferred to other parts of the fungus, either to actively metabolizing regions or to reproductive propagules. Fungi are rightly notorious for their extremely prolific reproduction, large numbers of dispersal spores often being produced very rapidly, and, equally important although less widely appreciated, large numbers of residual propagules being left behind in regions where mycelial growth has taken place. The cause for this prolific reproduction is partly the inexpensability of fungal protoplasm. Natural death of fungal protoplasm then is probably rather uncommon; it is mainly brought about by either enforced decline in metabolic activity by unfavorable environment in the absence of an appropriate response on the part of the fungus, or by a decline in the viability of inactive propagules by senescence. In nature any marked and rapid decline in the amount of viable fungal protoplasm is likely to be attributable to some environmental factor actively causing death. Factors having this action are considered later in this chapter.

It was indicated earlier that one consequence of the rapid and efficient colonization and utilization by individual fungi of substrata in nature is that their substratum may soon become unsuitable for those fungi. Natural substrata are often rather small, and almost always they are somewhat discontinuous in distribution. It is very rare for large amounts or areas of a particular decomposable material to be available at a site at the appropriate state of decay for any length of time. Where such a situation does exist, survival of a fungus might be ensured by continued somatic growth of hyphal apices, but since this situation is very rare the propagular modifications of fungal protoplasm serve a very important role in their ecology, and allow the transfer of the fungus from one available substratum to another. The nature, form, and position of dispersal propagules is often related to the habitat in a manner assisting efficient dispersal. Residual propagules are often larger than is the case with dispersal propagules

since they are dispersed in time, remaining static while the environment changes round them. If the environmental change with seral succession is completely unidirectional and progressive, the same type of substratum may not again contact the residual propagules, which will eventually die. However, in many terrestrial habitats, particularly in the later stages of seral succession, changes are cyclical, and there is some chance that a suitable substratum at the right stage of decomposition will contact the residual propagule.

What has been discussed here helps to explain the ecological significance to fungi of their ability rapidly to take advantage of a substratum or situation and to exploit it quickly, their very thorough and intimate association with the immediate environment, biotic and nonbiotic, their ability to survive relatively large discontinuities in the environment appropriate for their activity, and the wide geographical range of individual species. While these characteristics are of general significance to fungi, not all species possess all in equal degree. Fungi especially active in the early stages of substratum succession, for instance species of *Neurospora* and *Rhizopus*, show exceptionally high rates of growth and utilization, and a correspondingly rapid and prolific production of dispersal propagules. Other species, particularly some ascomycetes and basidiomycetes, active in later stages of substratum succession, grow more slowly, and have a generally low rate of metabolism and utilization, and are correspondingly more tardy about reproduction.

Of much advantage to fungi in their role of versatile opportunists is their high degree of adaptability. This is expressed in both morphologic and metabolic ways and can be mediated by three normal mechanisms—hybridization, genetic mutation, and environmentally induced, nongenetic variation—as well as by the two additional and peculiar mechanisms of parasexual recombination and the labile system conferred by heterokaryosis (Volume II, Chapters 18 and 19). Taken together these five mechanisms confer an unusually high degree of adaptability on fungi. Species can show variation in respect to the substrates suitable for supporting growth, tolerance to physical factors and different forms of biological antagonism, mode of somatic growth for different environmental conditions, and types of propagule produced under different conditions. Under the abnormally favorable conditions of normal laboratory culture fungal species exhibit a fair degree of constancy of form and physiology. In nature their lability may be much greater than the usual laboratory studies indicate. By altering the normal laboratory conditions, and by providing lower concentrations of nutrients, or more natural sorts of nutrients, even in axenic culture some idea of the potential range of behavior of a fungus can be obtained. In mixed culture in the laboratory a still wider range of behavior may be

observed. In addition to being less variable in laboratory culture a species may even show characters that would not allow it to survive in nature, and conversely may fail to show characters that would be positively advantageous in nature. Thus cultural forms of fungi not only may be less variable than the same species in nature, but may be in some respects morphologically and physiologically quite different. On continued laboratory cultivation fungi may become more or less permanently altered in form and metabolic behavior in a direction adaptive to the laboratory environment, which is both specialized in particular and unusual directions, and also less variable than environments in nature. Thus the characters of a laboratory strain of a species may have little significance for the natural survival and behavior of that species, but the phenomenon itself may be relevant to conditions in nature. Thus two laboratories starting with the same wild type, but using different media, cultural methods, or modes of transfer during subculture, may soon possess different morphological and physiological entities. So in nature a species may, owing to the different selective pressures of different niches, come to exist in more than one form, each being adapted particularly to its individual niche. Genetical clones of a fungal species are known to occur in soil in distinct forms in different environments (e.g., Durbin, 1959; Papavizas and Davey, 1962). In other situations a fungus species may in nature form a heterokaryotic pool from which peculiarly suitable adapted forms may arise by selection by particular environments (Buxton, 1960). One result of these phenomena is that cultural features by themselves are inadequate to properly describe an organism, and there is a need with fungi, as Winogradsky envisaged with bacteria, for a taxonomic classification that takes into account ecological as well as cultural features.

II. IMPORTANT CONCEPTS

The study of terrestrial ecology of fungi has during its development been particularly aided by the formulation of several concepts explaining some of the significant processes that operate. These concepts can also be applied to the ecology of other types of organisms, and therefore contribute to general ecological theory. The more important of these concepts are outlined here.

A. *Inoculum Potential*

The term inoculum potential has been used in plant pathology in more than one sense and the history of the term is set out clearly by Garrett (1960). The most useful meaning is that which Garrett (1956) defined as "the energy for growth of a fungus (or other micro-organism) available

for colonization of a substrate at the surface of the substrate to be colonized." The concept was first used in connection with the infection of hosts by pathogens. A host exerts a physical and chemical resistance to fungal penetration (the host resistance), and the chance of a fungal growing point successfully penetrating the host surface is better when it has a greater growth energy or inoculum potential. With active mycelium this may come about through better environmental conditions (for example, nutrition, or through more hyphae of the same sort attacking at one point). With a propagular inoculum larger propagules or more of them may give a higher inoculum potential.

Not only living hosts, but also dead substrata, can exert a resistance to colonization. This *substratum resistance* is equivalent in its ecological effect, if not in its mode of action, to the host resistance of a living organism. There are at least three possible sources of substratum resistance. First, it may be a residual host resistance carried over from the living host into moribund tissue for a limited period, in which case it will have its highest level initially and subsequently decline. Second, it may be a result of the production of external toxic metabolites by microorganisms already active in earlier stages of substratum succession, in which case it may fluctuate in intensity with time. Last, it may be due to an initial refractoriness in the substrate materials, and require a certain "starter" energy to be expended before any useful energy can be got from it. In this case the degree of substratum resistance may increase progressively during substratum succession as the more easily utilized substrates disappear. A saprophyte, in order to colonize the substratum, must have a sufficiently high inoculum potential to balance against the substratum resistance. The possession of a higher inoculum potential will permit the colonization of more difficult substrata.

B. Competitive Saprophytic Ability

This concept also has been discussed in detail by Garrett (1956, 1963). He defines it as "the summation of physiological characteristics that make for success in competitive colonization of substrates." The important point is that the colonization is competitive. Many fungi when in pure culture are able to utilize substrata that in nature they are unable to colonize. The reason for this failure in nature, and therefore for the more restricted range of activities there as opposed to laboratory culture, is that other more successful organisms are present, possibly gaining entry first, and certainly actively excluding the less successful organisms. This exclusion occurs as a result of antagonism, which is discussed on p. 13.

Garrett (1950) lists four general attributes that are likely to contribute to a high degree of competitive saprophytic ability. These are (1) rapid

germination of spores and a high rate of hyphal growth, both favoring rapid colonization; (2) good enzyme production, which favors rapid and extensive substrate utilization; (3) production of substances toxic to other organisms, which may reduce competition for the available substrates; and (4) tolerance of antibiotic substances produced by other organisms, this property enabling the fungus to be saprophytically active even in the presence of competitors able to produce the substances mentioned in (3) above. The first two of these characteristics will be advantageous in any circumstance where sufficient amounts of utilizable substrates are available to support a high degree of activity. This means, in effect, the early to middle stages of substratum succession. It has already been indicated that where substrates are available only slowly or in small quantity a low rate of metabolism and a correspondingly low rate of growth may be an advantage. The third property is probably of particular advantage in the very early stages of substratum succession where there are still few organisms present, and where the readily available energy-yielding material is at its maximum and may support the vigorous growth that can produce these substances. In later stages of decomposition more organisms will be present in the substratum, and there may be a relatively high level of toxic substances residually present together with those concurrently being produced. Under such circumstances the fourth property listed will be of most importance, its possession being necessary for activity before any of the other three characters can be exhibited.

The concept of competitive saprophytic ability has been much used recently and has stimulated a great deal of valuable work. Generalized statements of competitive saprophytic ability in respect of individual fungi can have broad validity. Thus it can be said that fungi of very low competitive saprophytic ability do not survive as saprophytes in soil generally, and therefore need some protection against the antagonism that prevents their successful activity there. Many such fungi depend upon a host for this protection, the host acting as suitable substratum and also excluding potential antagonists. The fungus has here exchanged tolerance to antagonism for tolerance to host resistance. Such organisms have been described by Garrett (1956) as *ecologically obligate parasites* in that, like true obligate parasites, they have no soil ecology, apart from a declining phase after death of their host. Similarly, in a general way a spectrum of competitive saprophytic ability can be envisaged among terrestrial fungi, those with a low value occurring very early in substratum succession and being pioneer colonizers, those with a higher value being able to be active later when mixed culture conditions impose more intense antagonism. However, too often the concept has been used in a vague sense and applied as though each fungus could be assigned an invariable value to apply under all

environmental conditions. In fact, the competitive saprophytic ability is not a fixed characteristic for each fungus, but may vary according to the particular environment presented. A fungus with a high competitive saprophytic ability in respect of the colonization of a newly dead plant root may have a low one for a newly available dead fly—different enzymes being involved. Similarly a leaf falling on a soil under one set of conditions of temperature and moisture may be colonized by quite a different microflora from that under other conditions. The immediate conditions influence the competitive saprophytic abilities of the different organisms available to colonize and thus affect the outcome of the selection. For many fungi that have been studied, and assigned on paper a high or low competitive saprophytic ability, we know next to nothing about the conditions under which the competitive saprophytic ability might in fact operate at that level, and how changed conditions might affect this level. A more precise statement of those conditions and how they do affect the competitive saprophytic ability is desirable in future work on this topic.

Competitive saprophytic ability works along with inoculum potential, each being a factor in the successful outcome of colonization. A high inoculum potential may allow a fungus to colonize successfully in the face of competition from another fungus of a higher competitive saprophytic ability under the given environmental conditions, but having a lower inoculum potential at that point.

C. Antagonism

Antagonism is the factor that makes for the difference between saprophytic colonization in pure culture and saprophytic colonization in nature where other microorganisms are present. Ecologically obligate parasites, unlike true obligate parasites, are, in axenic culture, capable of colonizing and utilizing dead substrata; it is only in mixed culture in nature that they are unable to colonize or survive saprophytically, and must depend on living hosts. Antagonism is important in terrestrial ecology also because of its role in substratum succession, during which substrata become progressively unsuitable for some colonizers. Along with affecting colonization and amount of activity after colonization, antagonism further affects fungal ecology by influencing survival after activity has ceased.

There are three main ways in which antagonism of one organism toward another can be expressed. *Antibiosis* occurs when one organism introduces into the environment a chemical substance that is toxic to and inhibits the second organism. *Competition* occurs when the two organisms compete for the supply of some feature of the environment that is present in quantities insufficient for both. *Exploitation* occurs when one organism

utilizes directly as food the body or part of the body of the second organism. Parasitism and predation both belong to this form of antagonism. All these categories of antagonism exist among fungi in nature, and Park (1960) has discussed in detail their relative importance in fungal ecology. It might here be noted that competition is used in two senses in the literature, one the strict meaning defined here, and the other a general meaning more or less equivalent to antagonism as used here. In most contexts it is possible to know which meaning is intended, but some care should be taken to understand this bifarious usage. It is important also to appreciate that exploitation is the only mechanism that operates by a direct effect of one organism on the other and from which the antagonist obtains direct benefit as a result of its action. The other two mechanisms, antibiosis and competition, operate indirectly through the environment and may therefore influence any other organisms in that environment. In most situations in nature large numbers of microorganisms are present in the environment and the outcome of the antagonisms is, as a result, extraordinarily complex. Probably the most significant form of antagonism in soil is that of antibiosis, not necessarily by specifically active antibiotics but rather by more generally produced toxic external metabolites. The widespread soil fungistasis that has interested a number of workers in recent years is most probably a summation of the production of such substances by the activity of microbes generally in the soil. Park (1967) discusses and explains some of these points in more detail.

D. Saprophytic Survival

Like saprophytic colonization, saprophytic survival occurs specifically under conditions of antagonism. Garrett (1944) used the term in connection with a parasite that had colonized living host tissue to describe its survival in an active mycelial form after death of the tissues of the host. Saprophytic colonization, by contrast, refers to the entry into already dead substratum material in the presence of antagonism. Most parasites that are not true obligate parasites probably survive for some time in an active condition in the tissues after death of the host, but the duration varies enormously with the species of pathogen, and is related among other things to its competitive saprophytic ability. While Garrett defined this concept of saprophytic survival in respect of parasites it can also be applied to survival of fungi that have previously saprophytically colonized a material. Caldwell (1963), in a study of fungi that over a two-year period colonized woody substrata in soil, has shown that some species appear, fairly rapidly reach a peak, and then decline in the frequency with which they can be isolated from the material. Other species appear gradually and remain more or less constantly present throughout an

extended period. As in the original concept, where some pathogens, in tissues colonized when living, continue activity after the tissue's death and show saprophytic survival, while others soon cease activity and persist, if at all, only by residual propagules, so saprophytic colonizers may be similarly differentiated in their behavior, some continuing saprophytic activity for long periods and so surviving, while others soon become inactive and produce resting structures.

Survival as inactive structures has been described as *dormant survival* as opposed to saprophytic survival, but it could be useful under certain circumstances to differentiate between survival of resting structures that on the one hand are truly dormant in the physiological sense of being incapable of germination owing to immaturity or to endogenous inhibition, and those that on the other hand could immediately germinate given favorable conditions but that remain inhibited by environmental antagonism (antibiosis). The term *inactive survival* can cover both these conditions, *dormant survival* being particularly appropriate for the first, and *inhibited survival* for the second. Related phenomena under the headings constitutional and exogenous dormancy are discussed by Sussman in Volume II, Chapter 23.

E. The Half-Life Concept

This concept was developed by Yarwood and Sylvester (1959). They stated that viruses and plant parasites in an unfavorable environment decline in numbers at a logarithmic rate, and that in such a situation there can be no accurate statement of the duration of total longevity. The size of the initial population, the slope of the curve, and the sensitivity of any methods for detecting numbers all determine the useful end point in the construction of a declining population curve. The sort of calculation made by these authors can be applied to a population of resting structures of a fungal saprophyte showing inactive survival in an antagonistic environment. There is no point at which one can say survival has ceased, but ecological survival will terminate when the inoculum potential of the population has fallen below that necessary for successful colonization of substrata that become available. In inactive survival, then, the effective time of survival is governed by the size of the initial population, the amount of antagonism and hence the rate of decline, the degree of suitability of substrata becoming available, their frequency, and the amount of competition for colonization of these substrata. During and soon after successful exploitation of substrata the inoculum will be high because residual propagules are produced by the mycelium. In nature, then, the numbers of an organism of this sort at a restricted site will, when represented as a graph with time, be a curve rapidly rising to a peak

and then more slowly declining to a trough with abrupt transitions between the rising and declining phases. The distances between the troughs represents the time intervals between availability of successive substrata. A steep decline of numbers in a habitat will necessarily be matched in any successful fungus by a steep rise to a high peak or by a relatively frequent substratum availability. A slower decline will allow a fungus to survive when substrata are less frequently available. Thus high resistance of residual propagules to the effects of antagonism and enforced decline is an effective adaptation to survival just as is a high rate of metabolism and reproduction.

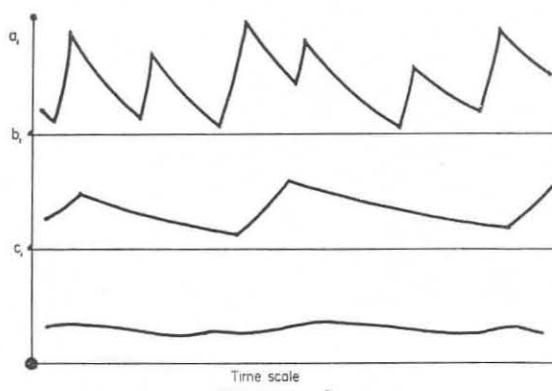


FIG. 1. Schematic population curves for fungi from different stages of substratum decomposition. Curve *a*: Fungi active in early stages of succession: high rate of metabolic activity and rapid reproduction, but rapid decline and need for frequent substratum availability. Curve *b*: Fungi characteristic of a later stage: less rapid reproduction matched by a slower decline and a greater resistance to antagonism. Curve *c*: Saprophytic survival in soil by fungi with somatic resistance to antagonism: no clear-cut logarithmic phases or half-life for inactive survival.

A high level of metabolism and reproduction is the adaptation shown by many early colonizers like *Neurospora* and *Rhizopus* described earlier, while the high resistance type of adaptation is that shown by species active somewhat later in succession and which take longer to mobilize substrates and to reproduce, but which also decline less rapidly. These types of behavior are diagrammed in Fig. 1.

High resistance to antagonism may be shown by somatic structures as well as by propagules, and this property may indeed allow lengthy saprophytic survival, in which case the half-life concept is not applicable. With organisms showing this adaptation the population curves with time may show some fluctuation but no clear-cut logarithmic trend. Warcup (1957), by isolating and identifying viable pieces of mycelium from soils and

studying their distribution with time found that some species showed short periods of activity and persisted as inactive propagules between these periods, the periods of activity corresponding to the availability of readily decomposable material. Other species, by contrast, were present as viable and probably active mycelium constantly throughout the investigation and showed no marked increase in frequency during the decomposition of plant residues.

III. FACTORS INFLUENCING FUNGAL ECOLOGY

In any local environment there will normally be several types of substratum, and each of these may have a number of microhabitats each with its characteristic and peculiar microbial community. Reasons of this sort have led students of fungal ecology to be very much concerned with the factors influencing behavior within microhabitats. The overall environmental factors as influences have, in consequence, been somewhat neglected. But the major and obvious factors in a local environment are important and should be considered. Garrett (1963) says, "In the ultimate analysis, it is the physico-chemical characteristics of a habitat that determine the kind of community that will occupy it. But the precise composition of that community at any time will be the result of competition between different species of organisms." The first determinants of a community are the nature of the substratum and the conditions prevailing around it. These will select from among the organisms available, favoring some at the expense of others, and excluding some altogether. Only then, among those that are able to develop, will antagonism operate in the second and most studied phase of the organization of community structure. The factors that influence the course of these developments of a community are of course largely the same as those studied by ecologists of other groups of organisms. The effects of these factors on individual fungi have been described in previous articles in these volumes. Nutrition is the primary factor of course. In many substrata more than one type of material is available and many fungi may be potentially capable of development. In a few substrata the commoner nutrients may be absent, and the dominant nutrient be suitable for only a small number of fungi. The colonization of such restrictive substrata can be of particular interest, but it is simpler in principle than that of most substrata. The availability of nutrients within a substratum as a function of time is, of course, not constant, but generally undergoes movement in one direction, namely toward more and more intractable and refractory substrates, and eventually tends toward nil. A substratum with a nutrient content unsuitable

for a particular fungus may, however, by the activity of other microbes, subsequently become suitable, as explained later, so that the trend is not uniformly toward lesser availability of food.

Temperature of the local environment has an important immediate influence in that fungi with limits outside the range are automatically excluded. There is also the less immediate effect whereby temperature will have some selective action among fungi whose acceptable range falls within that of the environment, those fungi whose optimum comes nearest to the prevailing temperature being favored most. In nature, of course, temperature is not static but fluctuates to some extent diurnally, and usually to a much greater extent seasonally. This contributes, along with fluctuations in other factors, to the common situation where habitats are rarely optimum for the same organism for very long, and may if the fluctuations are at all frequent and regular, give a cyclical pattern to the community.

Water is necessary for all forms of life. As an environmental factor it acts upon fungi in several ways, affecting directly as free water the growing mycelium. The amount of water also indirectly affects the availability of nutrients and the concentration of toxic substances. A drier situation may have a higher concentration of some nutrients, but also a higher concentration of some inhibitory factors. Humidity of the atmosphere is also important in affecting the morphogenesis of fungi. The nature and size of hyphae, their degree of branching, the intensity of sporulation, and even the type of reproduction, are affected by this factor. The nature of the substratum may also affect the water availability through its own attraction for moisture, some substrata allowing easier uptake by micro-organisms than others of the same moisture content. Mycologists who have been interested in this factor have usually characterized a soil by its moisture-holding capacity, a property which allows for some differences of this sort. Recently Griffin (1963) has reviewed the importance of water in the ecology of soil fungi and has argued that moisture-holding capacity is a poor criterion for comparisons between substrata and that moisture characteristics of soils should be more clearly defined. The criterion of moisture characteristic allows both for moisture content and also for the suction tension of the soil. Apart from this overall measure for soil as a whole little is known about the water retentivity and characteristics of different substrata within the soil. This is obviously an important property and an understanding of it would seem important in ecological studies. Osmotic pressure of the soil solution is probably not an important influence but when it is excessively high it may inhibit some of the water molds that can occur in normally moist soils.

The water content of soil may inversely affect gaseous exchange in soil

and associated substrata. Fungi, when active, consume oxygen and produce carbon dioxide. Gaseous diffusion in normal soil is somewhat restricted; in the presence of excess water the restriction is even greater. Penman (1940) has discussed these aspects in detail. Within soil the proportion of oxygen in the soil atmosphere is commonly lower than that in the air above the soil but, except under very wet or flooded conditions, is adequate for the growth and activity of most fungi. The lower concentration of oxygen in the soil atmosphere is less likely to be an important ecological influence than is the higher carbon dioxide concentration, which varies from 0.3 to 10% in reasonably porous, nonflooded, unamended soils but can rise higher on compaction, flooding, or with intense microbial activity (Griffin, 1963). Many fungi are markedly affected by higher carbon dioxide levels of the sort that have been recorded in soil, and this can be an important factor in selection of species composing communities (Durbin, 1959).

The pH of the substratum may have an important influence on fungal ecology. The overall composition of the microflora in respect of bacteria and actinomycetes, as against fungi, is related to this factor. The first two groups function better in neutral to alkaline conditions, whereas fungi show best activity under acid conditions. However, most fungi have a rather wide range of tolerance of pH and their growth curve over most of the range is somewhat flat-topped so that while an exceptional pH outside the range of some fungi may be an eliminative factor, within the range small changes may not have such a great effect as concurrent changes in other factors.

The overall physical and chemical characteristics of the soil may have a less direct effect than the characteristics of the substratum itself, but they are still extremely important in fungal ecology. Not only must temperature, moisture content, aeration, base-exchange properties, and pH be considered, but also mechanical properties such as soil texture, pore space, crumb structure and tilth which influence the magnitude of effect of some of the other factors, such as water and oxygen availability and temperature. In the case of this last factor a good tilth or a good organic content can shield the surface of the soil against the effects of insolation and can significantly reduce temperature at a short distance below the soil surface. It may also reduce in amount the deleterious effect of insolation acting as radiation, not simply as temperature. Direct radiation in high doses has a harmful and even lethal effect on fungi. Soil structure and texture also affect soil pore space. In respect to fungi not only is the total space important, but the size of individual pores and pore necks has an effect. With sufficiently large pore spaces fungi may reproduce more or less normally in soil as in laboratory culture, with conidiophores, etc. Where

pore spaces are small the development of these structures is not possible. Pore necks if very small may reduce the amount of spore dispersal in soil by water.

The biotic environment, which itself is also controlled in part by the physical and chemical factors listed, in turn influences the fungi present. Plants and animals may alter some of the other factors by providing or removing nutrients, substrata and water, by improving soil texture and tilth, by improving drainage and gaseous exchange, by increasing humidity and decreasing the water loss from the soil surface, and by reducing insolation at the soil surface. Larger organisms may also affect dispersal of fungal propagules, sometimes impeding dispersal and sometimes assisting it.

It has been pointed out that the factors operating in an environment are rarely constant but may fluctuate irregularly, oscillate cyclically, or show a progressive trend. The system is dynamic and the changes may be relatively great, with large alterations in the characteristics of microhabitats and hence of the microflora. Biotic influences in general confer a greater degree of stability on the microhabitats and reduce in amount the changes in factors within an environment. In other words the presence of other organisms has a buffering or damping effect. The result of plant and animal activities through root growth, leaf and stem shading, root secretions, burrowing, mixing, comminution and trituration, and the addition of debris as substrata is to reduce the spatial and temporal discontinuities which interrupt fungal activity, and to make environments more generally favorable for more fungi, and thus to increase antagonism. Man's actions fall into this category. However, the manipulation of soil by mankind tends even more than the activities of the other biota to make for uniformity by reducing the range of variation in microhabitats. It may even reduce the number of species that can survive, while allowing an increase in total biomass.

Not only do environmental factors act differently on different fungi, and thus operate in the selection of species available for community evolution, but they may also act differently upon different phases in the life history of a single species. Thus germination, growth, reproduction, dissemination and survival may not all be influenced in the same direction by a given factor at a given level. Germination is commonly more demanding in terms of many environmental conditions (but not always for nutrients) than is growth. Conditions inimical to growth may actually help to initiate and favor reproduction. Germination in dormant spores is sometimes stimulated by an extreme environment that would be most harmful to germ tubes and mycelium (see Chapter 17). Survival and dissemination occur under conditions that inhibit germination. An altera-

tion of environmental conditions between the production of a spore and its germination is almost always necessary, since spores often fail to germinate in the identical conditions under which they are produced, even in culture.

It will be seen from some of these different relationships that individual species and even forms of fungi have adapted themselves to the changing dynamic environment in which they occur. This is often particularly obvious in the case of reproduction, dissemination, and survival. There are obvious relationships between fungal morphology for these processes and the local environmental conditions. The timing of the phases of life cycles is also often particularly appropriate to changes in environmental conditions, particularly seasonal fluctuations. Adaptation of growth processes of individual fungi to special conditions is also found and is responsible for some of the unusual tolerances to extreme conditions. For instance, a few fungi are able to make somatic growth at unusually low oxygen tensions, e.g., *Blastocladiella pringsheimiana*, *Penicillium roquefortii*, and a number of yeasts. Others, such as *Fusarium oxysporum*, may grow at unusually high carbon dioxide levels. Some species, i.e., *Rhizoctonia solani* [*Corticium solani*] (Durbin, 1959) show a clonal differentiation depending on tolerance to carbon dioxide levels, and different clones occur at different depths in soil. Adaptations to biotic factors is common. Disease-causing fungi exemplify this particularly well, but similar biotic adaptations may occur in nonpathogens. Adaptation to the seed-borne habit is very helpful to a fungus in assisting dispersal and the finding of a substratum, and not all seed-borne fungi are pathogenic for their carrier species. *Serpula lacrimans*, while not a pathogen, can cause considerable economic damage to man's economy by its destruction of timber, and this species is fairly uncommon outside man's economy. It is adapted to the more or less equable temperature and the protection from draughts that buildings provide. Pigmentation, particularly of dispersal spores, is an effective and rather common adaptation to tolerance to radiation, and the same adaptation occurs in mycelium of fungi growing habitually in situations where they are exposed to radiation (see Volume I, Chapter 24). In forests, where airborne dispersal may be less effective than in open communities, a number of characteristic basidiomycetes and ascomycetes fructify underground and are adapted to dispersal by subterranean animals rather than by turbulent air currents. On mountains at high altitudes some basidiomycetes have xeromorphic fruiting bodies which show spongy layers, small size, resupinate habit, hard context, and occur low on the host tree, particularly in clefts in the bark. By adaptations such as these particular fungi have extended their range of tolerance to certain environmental factors.

IV. DISTRIBUTION OF FUNGI

Review accounts of the geographical distribution of fungi have been written by Bisby (1933, 1943), and there is also a useful account by Wolf and Wolf (1947). These accounts and Chapter 18 of this volume should be consulted by anyone interested in the topic. It is, however, clear that relatively little detail is available that helps toward a general knowledge of fungal distribution in the world as a whole. Reliable information depends, of course, in the first place on the world distribution of mycologists, which itself is far from even, and many of these have special interests rather than general ones. A second limitation is that much of the information that is available comes from collections and records only, and little work has been done to supplement it by analytical studies of the factors affecting the activity and appearance of individual fungi or groups of fungi. Moreover for many fungi, particularly agarics, gasteromycetes, and many ascomycetes, the records or collection data are of sporulating stages only, and although these do depend on some prior activity this can be misleading since conditions for fructification may be rather different from those for vegetative activity and may give a one-sided picture. For some fungi even the habitat for fructification may be different from that for somatic and trophic activity. This is seen clearly in some of the slime molds which migrate to a suitable place for fruiting. Perhaps the one valid generalization on distribution that can be made is that many fungi are extremely widespread. An example of this is the fact that there are more total phanerogams in the world than described species of fungi, but in any one area there are almost always more fungi than phanerogams. Spores and propagules are produced and dispersed very efficiently (see Volume II, Chapters 21 and 22), and resting stages are often long-lived. The fungi are dispersed by the natural agencies of air and water, on seeds, by animals and human agencies over very large, often worldwide, areas. Where conditions are suitable the fungi arriving may be successful. Distribution therefore depends more than with most organisms on local conditions, and where favorable conditions occur, there the fungus is likely to be found. There is no good evidence that fungi are limited geographically by barriers to dispersal as is often the case with higher plants and animals. Even fungi of special habitats which, in consequence, are only occasional or even rare, may nevertheless be widespread. Pugh and Mathison (1962) discuss the widespread occurrence of certain keratinophilic fungi even in soils in which keratin is difficult of access. Some fungi are widely distributed even where the mode of dispersal would not seem obviously well adapted to this end. Thus the water mold *Allomyces arbuscula* occurs

in soil from all continents. Although it is relatively rare to find endemic fungal species they do occur. *Phymatotrichum omnivorum* is a plant pathogen that is confined to the southwestern United States. Similarly the human pathogens *Histoplasma capsulatum* and *Coccidioides immitis* occur in restricted areas of the United States and elsewhere. In these examples, however, the extreme localization is related to particularly suitable local conditions for activity and survival, and not to any limitations of dispersal.

Substratum is one of the most obvious determinants of distribution and must be the primary factor in world distribution of fungi. This is seen very clearly in the case of pathogens where their range does not extend beyond that of the hosts and may be limited further by other environmental factors that are not favorable. Hosts are commonly able to grow in regions outside those favorable for the development of the pathogen. The same considerations apply also for saprophytes. The distribution of coprophilous fungi, for instance, is related to the distribution of herbivores of the correct habits and constitution. Saprophytes are usually less specific in substratum requirements than are pathogens, so saprophytes in general have a wider distribution than pathogens. But since the nutrient condition of the substratum is only one of the relevant factors a particular substratum may support different fungal populations in different areas. In this respect immediate local differences may be greater than continental differences. It has for instance been estimated that more than 70% of North American agarics and polypores are also found in Europe, but that latitude exerts an important influence on the distribution of particular common species within these two great areas. Thus *Stropharia depilata* is boreal in range while *Amanita caesarea* is temperate, each occurring in both continents. Gasteromycetes tend to be widely represented in both the Eastern and Western hemispheres, particularly in dryish areas, but the group shows a pattern whereby the Lycoperdales is mostly temperate while the Phallales is predominantly tropical. Similarly in the Ascomycetes members of the Xylariales in both hemispheres are more common in the tropical zone than in temperate and cooler regions. The fungus:bacterium ratio of the microflora of soils, independently of geographical area, increases from the equator toward higher latitudes. Temperature may be one of the factors in these general correlations, but few detailed studies of the conditions necessary for different phases of the life histories have been made. Such studies are essential for reasonable interpretation of some of the observations concerning geographical distribution.

Since it is local conditions that are primarily important in this connection, it is not surprising that large discontinuities occur in the distribution of some species. Where the appropriate conditions occur, the fungus is likely to be found despite its absence from intermediate regions. Desert

soils all over the world have a basically similar fungal population, with a high proportion of species from the Dematiaceae and Sphaeropsidales. High mountains all show common features, the fungi of alpine regions in lower latitudes resembling those of the arctic regions, and showing more micromycetes than macromycetes.

Some of the recorded discontinuities in distribution are extremely large, and often mycologists have been impressed by the appearance of a fungus in one place at one time and then its absence or apparent absence for quite long periods before its next recorded appearance. *Urnula geaster*, an ascomycete with a very distinctive and striking fruit body, and a very obvious species, was recorded from Texas in 1893, and next in Japan in 1938. Another ascomycete, *Sarcoscypha minuscula*, is recorded only from Portugal and from California. Temporal discontinuities can be great, even in one continent. *Eremascus albus* was first described in Europe in 1883 and then not reported again until 1950. Although examples like this may represent extremes of the natural dynamic and changing situation, and be due to local and sporadic occurrence of conditions suitable for activity, it is more probable that incomplete recording is responsible. Other members of the family containing the two discomycetes mentioned above are far from frequently recorded fruiting. The reliance with many fungi upon records of fruiting structures is a serious disadvantage to their study. Distribution can be much more readily studied with those fungi that can easily be isolated in culture from active or resting stages in soil or other substrata. Such isolation methods give a much more reliable picture, and for many fungi where these methods have been used the history is one of wide distribution with only sporadic activity when conditions are appropriate and the substratum is in the right stage of decomposition. For the remainder of the time, survival occurs as a resting stage or by dispersal of a large number of usually small propagules which find the appropriate substratum at another site.

A number of commentators on fungal distribution have pointed out that some species show a considerable amount of permanence at a site while others are essentially transient. This may reflect a true state of affairs in that some sites provide a rapid succession of a fairly limited range of substrata, whereas others show wide fluctuations in the types of substrata that become available. This last condition of low site stability is particularly common in the early stages of environmental succession. Another factor that could contribute to these differences is that some fungi have broad limits for substratum and other conditions, whereas others are very restricted by the need for specific requirements. Differences of this sort could account for some of the differences between "settlers" and "tourists," but it is more than probable that some of the described contrasts

are the result of differences in reliability of methods for detecting occurrence. Better methods for isolating and detecting individual fungal species could rapidly lead to a better understanding of their behavior in respect to breadth of distribution and constancy of occurrence in sites.

V. SPECIAL HABITATS AND HABITAT SELECTION

The variety of terrestrial habitats occupied by fungi is extremely large, since fungi are notorious as versatile opportunists, and almost anything that can be decomposed to yield energy will find some fungi able to colonize it. There is no point, therefore, in attempting to describe comprehensively the unusual habitats that are known to support fungi, but an account of some of these might be useful and illustrative of certain features. In this connection it should be emphasized that habitat is not substratum only, but includes other features. Any habitat that remains available for colonization for any length of time, say more than 1 or 2 days, develops a community that is more or less characteristic of it. This community comes about by selection, as described in more detail in the next section, but it is relevant here to note that the main selection may initially operate from the nonfungal part of the habitat. This is particularly the case when the habitat contains some unusual feature, such as a refractory substrate, or some toxic compound that limits or prevents the growth and activity of most fungi, but to which some fungi are or can become adapted. The study of such special habitats can be particularly interesting, and there are not usually any great difficulties since appropriate selective isolation techniques based on the special features of the habitat can generally be devised. An opposite type of situation arises in the development of community structure in relation to a habitat that is initially potentially suitable for any of a large number of available fungal species. Here the selection operates through factors from the fungi and other colonizing organisms, through processes of antagonism, so that some of the colonizers become successful and others are eliminated, while still others may be prevented from making any headway. Here, biological antagonisms, rather than habitat features, serve the formative role of integrating the community and determining its composition. It is in such habitats that the most complex biological interplay occurs, and its outcome may be very difficult to elucidate. Habitats of both sorts may progress through stages serially, and show a more or less well defined succession, but such a progression of stages is more particularly characteristic of environments in which the habitat itself initially exerts little significant selection. It is in such general habitats that the phenomenon has been most studied, and discussion of it is reserved for the following section.

Living tissues of organisms can be regarded as one special habitat of the type being considered here, the colonizers being parasites. Fungi that parasitize plants or animals have been extensively studied. The substratum here is clearly unfavorable for activity of most fungi, in fact, the host resistance of the animal or plant serves just that end, to eliminate by chemical or mechanical means most microorganisms in the environment. But certain fungi as well as some bacteria are able to overcome, avoid, or tolerate these defense mechanisms and to use the host as their substratum. Details of these relationships are given in Chapters 6, 7, 8 and 9. However, when the host defenses are completely overcome by the fungus, the invader may rapidly cause death of the tissues and the habitat then becomes general and open to colonization by other fungi. In associations where the fungus remains under a degree of control by the host defense mechanisms, yet is somewhat active, then it often occurs as the sole microbial occupant of that substratum. This is a very special habitat and one in which there is no microbial antagonism at all. Correlated with this is the fact that fungi adapted to this role are often found to be those most sensitive to microbial antagonism and appear therefore to depend on the host resistance as a protection from other more successfully competitive fungi. This situation may be true also of fungi from other "special" habitats. During evolution toward tolerance to rigorous and exclusive habitat factors, there has been a reduction or even an absence of selection pressure for tolerance to microbial antagonism, and such tolerance usually is found to be low in fungi typical of special habitats.

Fungi need not be parasitic and endophytic in a host organism to have a special habitat provided by that organism. At the surface of living organisms is a region that is intermediate in its selective action. Conditions here may favor some fungi and exclude others, so that special niches arise. Thus, at the surface of plant roots there is the rhizosphere effect giving an often characteristic flora. On leaves there occurs a similar and analogous phyllosphere effect. The rhizosphere has been a topic of interest since the turn of the century, and most work on it has been done with bacteria, but there is abundant evidence for selective effects of the rhizosphere on fungal populations about the roots of plants (Starkey, 1958). The roots of plants alter the soil by secreting substances that can act as major or minor nutrients, by sloughing off dead parts and by parts dying, by altering the pH, by altering the CO₂:O₂ ratio, by secreting toxic substances (host resistance), and by removing substances from the soil. The sum of these effects, each of which may be small, alters the soil and in turn the microflora. The most obvious result is a usually higher number of microorganisms in the rhizosphere region, and the difference between this number and that in normal soil is given as the R:S ratio. But there are

qualitative as well as quantitative differences between the two populations. Thus some fungi are inhibited by particular secretions from plant roots, while others are able to develop and may be stimulated. These quantitative and qualitative differences may be important to the higher plant. Not only may different species of plants affect soil differently and therefore possess different rhizosphere floras, but different cultivars of one species may also have very different effects. There may be among the fungi comprising the rhizosphere flora a fairly high proportion potentially pathogenic to the supporting plant. Species of *Alternaria*, *Fusarium*, *Helminthosporium*, and *Pythium* are commonly isolated from this habitat. This might be expected on the basis that those organisms have some degree of tolerance to chemicals conferring host resistance. In some investigated cases, however, root secretions favor organisms antagonistic to pathogens and thereby promote the development of a rhizosphere flora that helps to protect against infection. In this way some forms of host resistance are based on the rhizosphere effect.

Plant leaves, like roots, secrete substances from their surface, and spores fall on leaves. There they may be inhibited or may be able to develop. Most do not develop but some do but without being able to penetrate internally or cause disease. These constitute the phyllosphere population, which appears to be more restricted in numbers of species than is the rhizosphere, and is certainly more clearly defined physically in that there is not a continuous gradient outward from the surface of the organ as there is in the rhizosphere which makes the delimitation of zones difficult. In the phyllosphere yeastlike, budding forms seem to have an advantage, and the commonly predominating fungi possess this property. The mirror yeasts, *Sporobolomyces*, *Bullera*, and *Tilletiopsis*, and the mycelial fungi *Aureobasidium* and *Cladosporium* are particularly common on leaf surfaces and occur also on the bark of twigs and branches. The number of the fungi in these habitats is relatively low during the early part of the life of the organism but increases rapidly with aging of the organ and reaches its maximum at death of the organ. The increase is probably connected with the increase in humidity in the lower, more crowded parts of the plant, with the increasing amount of nutrients excreted, and possibly with the decreasing potency of the host resistance mechanism. Ruinen (1961) has reviewed the facts published on this habitat.

The surface of animals can also form a special habitat. Most fungi are excluded from this type of site by chemical secretions, but a few find a favorable niche which is thereby relatively free from antagonism. Dermato-phytes (see Chapter 8) that inhabit the keratin of hair, nails, or the horny layer of skin are often considered to be parasites, but are by analogy more like a dermosphere flora in their ecological relationships living on dead

tissue at the surface and being protected from antagonism by an unusual site. A number of yeasts also inhabit animal surfaces. *Lipomyces starkei* can under moist conditions develop very quickly on man within a few hours of bathing. *Candida albicans*, while most dramatic in its disease-producing role, is usually a commensal on moist surfaces of the human body and is able to tolerate the chemical conditions that exclude most other fungi.

The special habitats discussed so far in this section represent selection by exclusion of the majority of available organisms by toxicity of the substratum. The second major category excludes by providing a substratum that is suitable for a few specially adapted fungi but unsuitable by its lack of appropriate nutrients for the majority. Lignin is a substance that fairly few microorganisms appear able to decompose on any significant scale. Nevertheless among the species of fungi that cause tree diseases and decay of timber there are, in addition to those causing brown rots (corrosion rots) by the removal of cellulose, those causing white rots (destruction rots) by removal of lignin as well as much, if not all, of the cellulose. White rot fungi are not usually found to be active in general habitats: timber and related substrata form their special habitat. Not only do they display special enzymatic properties, but they form strands or rhizomorphs that help to provide a high inoculum potential since some starter energy is commonly necessary to get the process of decomposition initiated. The fungi in this category are mostly basidiomycetes, particularly agarics and polypores.

Keratin is another substrate that in nature supports a rather limited and defined fungal flora. Feathers, hair, hoof, and horn occur infrequently but nevertheless consistently in some natural sites. Some chytrids are found inhabiting these materials but more characteristic are the ascomycetes, *Onygena equina*, *O. corvina*, *Gymnoascus gypseum*, *Ctenomyces serratus*, and those members of the Fungi Imperfici associated with these perfect states, i.e., *Keratinomyces ajelloi*, *Microsporum gypseum*, and *Trichophyton terrestris*.

Paints and plastic surfaces are relatively resistant to decay, but, not uncommonly, in use they show some decomposition by a number of characteristic fungi, particularly *Aureobasidium pullulans*, *Phoma violacea*, and *Cladosporium herbarum*. At least one of the properties necessary for success in this habitat is resistance to desiccation and to radiation, a property needed in common with the population of the phyllosphere and of soils of deserts. The fungal flora of all three habitats have species in common. The fungal flora of paint must also be able to withstand toxic substances and to derive nutrients from it, although experiments have shown that at least some of the nutrients come from other sources such

as wood underlying the paint. Thus painted glass surfaces were shown not to support fungal growth. References to this topic are given by Reynolds (1950) and Eveleigh (1961).

Fungi are extremely adaptable, and even for seemingly most unlikely substrata there is usually some fungus that can decompose them and make some growth. Particularly in laboratories is it easy to acquire a collection in almost pure culture without special precautions as to sterility, as for example, in reagent solutions exposed to contamination for some time. Recent collections by the author include fungi growing reasonably well in 0.1 M citric acid, in 1% tannic acid, and in 10% Tween 80. In cases like these not only is the fungus able to use some of the unusual substratum for energy, but also it has a tolerance for it that other fungi may not have. Under such conditions it is probable that partial starvation growth is occurring, the fungus moving the cytoplasm forward within the growing hyphal tips and synthesizing new cell wall material, leaving empty cell walls behind as described earlier. Some fungi are able to make visible growth under conditions often surprisingly low in nutrients. Under humid conditions apparently clean glass may support fungal growth in this way, and in the tropics lenses may be damaged permanently by the etching effect of secretions from fungal hyphae (Smith, 1946). At the opposite extreme there can be selection by high concentration of nutrients. A few fungi are osmophilic and can grow, and in fact sometimes grow best, in solutions of high osmotic pressure. Some species of *Aspergillus* and *Penicillium* show this well, and are found growing on substrata like jam, leather, paper, where there is little free water. *Aspergillus glaucus* is common on dried fruit in damp cellars and larders. Some species of yeasts are typically osmophilic, particularly species of *Zygosaccharomyces*, some of which can grow in saturated sucrose solutions and in the free water condensed on honey or sugars. *Eremascus albus*, which grows well in a 40% sucrose solution, is known from culture collections as isolates derived initially from moldy damp mustard powder in 1950. In the examples of low and high osmotic pressure of the substratum, it is not the type of nutrient that selects and determines the colonizers but its concentration. Nonnutrient selection may operate also in other special habitats. Thus special thermal substrata such as composts and hay, that under moist conditions show "spontaneous" heating, possess fungal colonizers that can be active at higher temperatures than most fungi. Species of *Chaetomium* are commonly found decomposing cellulose in hot compost heaps, and *Aspergillus fumigatus* is particularly characteristic of overheated hay. Thermophilic fungi are discussed in Chapter 4 of this volume.

Special habitats, then, seem to be characterized by having one or more features unsuitable for fungi generally but to which a relatively small

number of fungi is adapted. Selection is thus immediate and is based on habitat factors; the community that arises does so by its species possessing in common certain properties adapting them to the special conditions. The selecting and limiting factors may be chemical, like nutrients and toxins, or physical, like temperature, moisture, or osmotic pressure. In some special habitats the initial limiting factors may fail to persist, either for natural reasons as when high temperature subsides in compost, or as an autogenic result of the microbial activities of the selected flora in the habitat, as when toxic factors are converted to inert compounds, or refractory substrates are converted to those readily available to more organisms. In such cases a special habitat may become converted into a general habitat and the potential flora is then no longer limited by the original habitat factors but may be selected from a wider field.

Most dead animal and plant remains or debris that become available contain a variety of carbon sources and other nutrients, and exist at a normal temperature, pressure, and range of moisture, and usually form a general habitat. However, deriving as they do from living and therefore special habitats these substrata may show the transition just described, and soon become colonized by typical members of general communities. Dung of herbivorous animals is a material typically of a sort available to most microorganisms yet it anomalously shows a very special flora that has interested large numbers of mycologists. The reason for this apparent anomaly is the treatment the material has had before being voided by the animal. The high temperature and the digestive enzymes have largely sterilized the material, leaving viable fungal spores of just a few resistant species that had been ingested with the plant food. These species contain members specially adapted, first in having devices to increase the chance of being present on the vegetation that is ingested, and second in their tolerance of conditions in the alimentary canal so that they begin to germinate while still in the hind gut. Thus when the dung is voided these fungi have already made some growth, and in fact are exposed to little antagonism from other organisms. The first colonizers have a large advantage, particularly when, like these forms, they have a rapid growth rate, enzyme production, and utilization of substrates. These special communities are of coprophilous fungi belonging to taxonomically very different groups and show wide morphological differences, but they have important biological and ecological features in common; these include (1) phototropic responses of the reproductive parts which assist in the dispersal of the spores from the humid crevices of the substratum to the surrounding vegetation; (2) large and often deeply pigmented spores, often in mucilage and difficult to germinate in the laboratory, but resistant to the digestive juices of the herbivores and, in fact, sometimes actively stimulated to

germinate in the gut. This special community, then, develops not because of especially appropriate conditions of the habitat at the time they are visible to the mycologist, but because of the earlier history of that habitat.

Another habitat that would superficially appear to be generally favorable, but that commonly has a set of special fungi developing, is burnt trees or wood and burnt areas of ground. *Anthracobia* spp., *Pyronema* spp., *Daldinia vernicosa*, and *Nummularia bullardia* are typical examples of fungi having the pyroxylophilous habit. Here the partial sterilization effect of heat may be analogous to the situation described in dung. Again the habitat eventually becomes open to a wider variety of colonizers, and becomes a general habitat.

VI. GENERAL HABITATS AND SERAL SUCCESSION

A. Substratum Succession and Seral Succession

General habitats proper differ from special habitats in that they show little special selectivity for certain species initially. In the early phases of their colonization chance determines which species arrive at the surface of the substratum, and it is in the later stages that the community structure, through antagonism and symbiosis, arrives at a more or less integrated condition. The changes that occur may be complex and constitute a continuous process, with a balance among various different forces. Soil, with the litter and debris accumulating on and in it, serves as a good comprehensive example of the general type of habitat. The habitat develops serally from the initial or parent stages by succession, and an understanding of ecology in such a habitat can best be gained by first considering the process of this succession.

With microorganisms there are two distinct levels at which succession can be considered. When a potential substratum becomes available for colonization in an environment a succession of organisms usually colonizes it. This is *substratum succession* and occurs on a small scale within a larger environment. Substratum succession represents a cyclical and continually occurring series of events within the larger system. On the other hand, a whole habitat starting from parent rock material also passes through a succession of phases before arriving at a more or less mature stage. This is *seral succession* and within such a succession a procession of fungal changes occurs often concurrent with and correlated with the changes occurring in other biotic properties of the habitat. Such succession may be primary, when the basic substrata at the start contain no microbially converted material, or secondary, when such material does exist. Secondary seral successions usually occur following some sort of partial or complete sterilization of a habitat by agencies like fire or flood, and the course of

succession and the main fungal participants may be very different from those occurring in a primary succession.

B. Primary Sere

The primary succession starting from bare parent rock is determined in its course, and the phases through which it progresses, by the following factors: (1) the nature of the parent rock, (2) the local climate, and (3) the organisms available. Fungal spores are among the first potential colonizers of parent rock since fungi have such efficient dispersal systems. Spores and other propagules are carried in by air currents, water (irrigation, flood, and drainage from higher areas), and birds, insects, and large and small soil animals. Some of these propagules may germinate and produce some mycelium, but mostly there will be very little in the way of suitable substrates, and in consequence spores and resting stages are the dominant elements of this initial phase, the fungal population being largely inactive. The species present at first are likely to be those in nearby habitats, particularly those with high spore production and with efficient spore dispersal, most especially dry spore forms carried in by air currents. Slime spore fungi and mycelial forms might be expected to be less frequent initially, being brought in later on wind-blown soil dust, on seeds as seed-borne fungi, and on debris carried by irrigation or flood, or by animals. From the random selection of the fungi casually available by these agencies there occurs further selection for those able to survive starvation conditions and the physically and chemically unfavorable factors that may exist. Extremes of temperature, water availability, radiation, pH, salt concentrations, and other toxic factors are very common in such habitats in the initial stages of colonization. The longer the period that elapses before the arrival of suitable substrata or of autotrophic organisms able to provide substrata, the greater the selective effect of the environmental factors and also the greater the range of species arriving on which these factors can act. In these early stages the habitat compares well with a special habitat in that selection of community is by extrinsic or habitat factors. Fungi tolerant of the existing unfavorable conditions will come to predominate. Selection here, however, will operate on inactive phases, rather than on the active phase as happens in special habitats. From these considerations it is seen that efficient and widespread dispersal, ability in the inactive state to withstand adverse physical conditions, and tolerance of starvation conditions will be the features most characteristic of the fungi found in this phase of succession.

The change from the bare parent rock and the increase in organic nutrients in the environment derives, of course, mainly from the activities of higher living organisms. In their effects on succession it is convenient

to separate the effects of the dead organic nutrient material from the effects of living organisms themselves. Dead nutrient materials arrive in any of several ways. The larger animals pass over the area and die, leave droppings or shed parts of themselves. Smaller animals may from adjacent areas move through the soil and underneath the surface and similarly add their bodies or parts thereof to the rock material. Plant parts—leaves, twigs, fruits, and seeds—may be blown in from elsewhere. Along with available substrata of this sort there may come additional fungi, as in the case of dung or leaves, that may be well adapted to the substratum but not necessarily to the habitat. Thus specialized fungi may grow and fructify but may, in the absence of vegetation, find little future for survival. The fungi already in the habitat and lying inactive will be stimulated into activity and attempt to colonize such substrata as arrive. The number of species, as of individuals, present in the early stages will be quite low, but organisms able to germinate, grow rapidly, and utilize the readily decomposed substrates as quickly as possible will have an advantage, particularly if they can then produce a crop of further propagules able to rest until another substratum arrives. Possession of some of the properties contributing to comparative saprophytic ability are of direct advantage here. In addition if some of these organisms produce an antibiotic substance to which others are susceptible these producers may appropriate a greater share of the available energy. It follows, of course, that other organisms similarly tolerant of the antibiotic substances, though not themselves antibiotic producers, will also benefit by the removal of any potential competitors sensitive to the substance. The characters conferring an advantage in the early stages are those listed by Garrett for competitive saprophytic ability. Slow growers will be at a disadvantage unless they are able to utilize the more complex compounds after simple substrates have disappeared. Even then relative efficiencies will still be important in selecting among fungi having the ability to utilize more refractory substrates, but as substratum succession progresses fewer fungi will have such ability so the intensity of competition, and of antagonism in particular, may decrease. The secondary colonizers may include not only organisms able to decompose more difficult carbon sources, but also organisms requiring more specialized compounds, such as vitamins and growth substances not initially present in the substratum but synthesized by earlier colonizers. Kendrick and Burges (1962), in connection with the decomposition of pine needles on forest soils, have shown that the substrate conditions may improve for a time for some fungi. The mycelium of fungi active in the earlier stages will form substrata for yet other organisms; some fungi are parasitic on other fungi, and dead mycelium may be utilized in part by other microorganisms. Later colonizers may thus be dependent on early

ones appropriately to modify the substratum. Animals such as nematodes, mites, the Collembola and millipedes may find in fungi a source of food. Other fungi in turn may utilize fecal pellets, dead bodies, and even the living animals as substrata. The community becomes more complex, and at the same time more sheltered from the bare physicochemical features of the environment. Fungi become less exposed to extrinsic environmental factors and more subject to intrinsic community or substratum factors. There arises a situation where organisms are dependent upon other organisms and influenced by them. The influences can be positive or negative, namely symbiotic or antagonistic; both are important in organizing the community.

The major substrata, of course, do not all arrive as dead materials, and living organisms in the environment play a very significant role in providing and modifying living conditions for fungi. Algae, animals, spores of thallophytes and archegoniates, seeds of higher plants, may all arrive. Some may be highly unsuccessful, particularly in the very early bare stages, and may die and therefore act merely as dead nutrient additions, but as the habitat becomes more and more modified from the parent rock, and fungi and bacteria convert dead nutrients finally into humus, the habitat becomes more favorable for autotrophic plants, and then for animals. The usual progression with ecological succession is to permit growth of more demanding organisms. These later colonizers are usually more complex and add more variety in the way of substrata.

Among the first successful autotrophic newcomers may be algal cells. Some may form lichens with fungi and thus contribute to the available energy in the area, others may grow without any such close association but nevertheless benefit fungi growing nearby by a sort of rhizosphere relationship. Then bryophytes and pteridophytes, and also more tolerant pioneer forms of angiosperms will appear. Subsequent arrivals are usually larger and more rapidly growing, and therefore provide more in the way of decomposable substrata. They provide a greater constancy in availability of substrata for fungi. Higher plants may also bring in with them, or be followed by, other fungi specially adapted to them. These include not just pathogens but also mycorrhizal species and commensals. As more organic materials appear, the environment can support more soil animals. The community evolves toward a more and more integrated complex, and the habitat becomes increasingly buffered from the physicochemical surroundings and more conditioned by the activities of organisms that are there. The sum of these activities, together with the residual effects of the original habitat and climate, gives a selective effect different from that originally obtaining, and with more emphasis on intrinsic factors. The first colonizers may not now survive since quite different properties are selected

for. Resistance to desiccation, insolation, variations in salt concentration, and starvation, are much less important than the four characters of competitive saprophytic ability listed earlier. The environment, having less variability than in the first place, has, therefore, fewer species of fungi. There may, however, be a greater number of individuals, that is, a greater fungal biomass. This also intensifies the antagonisms in the environment, and emphasizes further the selective pressure on tolerance to antagonism rather than selection for efficient dispersal and long-lived resting stages which may, however, still have some importance.

As seral succession progresses there is usually a smaller fluctuation in the range of environmental factors, the organic material becoming available will also be more constant in type with the increasing integration of the higher flora and fauna, and there are likely to be fewer temporal and

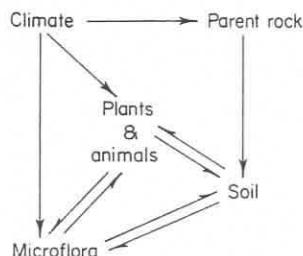


FIG. 2. Ecological interrelationships between soil microflora and the other components of the environment.

spatial discontinuities. At each seral stage the fungi present become, through selection, more and more related to the conditions, chance occurrence playing a smaller part so that the microbial community becomes integrated from within. There develops an intrinsic regulation of community structure. In this regulation the important operative influences of the habitat on the fungi include plant effects such as mycorrhizal and parasitic relationships, rhizosphere and phyllosphere effects, as well as the provision of dead plants and parts of plants. Also animal influences upon internal and external parasites and commensals, provision of substrata in droppings and shed parts, and dead animals take place. Both animals and plants also affect soil formation and thus the nonbiotic habitat factors. Humus formation and the accumulation of organic matter, aeration, drainage and mixing of soil are all affected. There is also the buffering effect of animals and plants on the climate of the habitat as described earlier.

During *seral* succession, therefore, there is an evolution toward a fairly characteristic sort of community, and toward what can be regarded as a climax, with an increase in biological energy and an increase in the total

biomass within the habitat. The climax is often relatively stable, but a change in any part of it may be reflected through the whole of it, because its ecology is that of a single complex interlinking system. Figure 2 illustrates the interrelationships between the elements of this system.

C. Secondary Sere

A secondary sere occurs in an area where at least some of the changes from parent rock to mature soil have already taken place, but from which all or most living things have been removed by some agency, which may also have caused some alteration in the physical and chemical characteristics of the habitat. High temperature, extreme desiccation, anaerobiosis, flooding, and scouring are the principal agencies that convert primary seres into secondary ones. The habitat at the start of a secondary sere is of course very different from that at the start of a primary sere and is commonly more favorable for activity than is the bare parent rock. This leads to a higher degree of intrinsic selection at first, and a more rapid evolution away from the chance assemblage of species toward an adapted and fitted community. Since the underlying rock and the climate have usually not altered, the sere may move back into the lines that were being followed by the primary sere, but this is not always the case.

Tutin (1941) has defined the climax as "vegetation which is in complete equilibrium with its environment" but states that this is largely a theoretical concept and in practice is applied to communities that to the observer give the appearance of being stable. The short life cycles and rapid metabolism of fungi give them in individual substrata a low degree of stability. The changes are rapid, continuous, and readily observable. It is therefore difficult to find any validity in this concept of climax in respect to fungal succession in individual substrata. Garrett has said that fungal succession is a progressive depletion of a habitat, and moves not toward a climax but toward exhaustion of energy. In respect to the whole habitat, however, substratum succession is a fluctuating or cyclical process in that it is continually being repeated on the same type of substrata by the same species of fungi. In the larger habitat many different stages are present at one time, and on this scale the same overall picture is seen at different times, and there is a gross form of stability for the whole habitat and, therefore, for the fungal population in the habitat climax can have a significance as useful as for that of higher plants, since its overall pattern is relatively constant. This climax stage is characterized not just by relative stability but also by its higher total biomass for fungi as for higher organisms.

Studies of succession on substrata have been made for a few types of substratum (Caldwell, 1963; Griffin, 1960; Pugh, 1958; Watling, 1963;

Webster, 1956), but relatively few studies have been made of fungal habitat succession, though some indications of the type of phenomena discussed here are available in papers by Webley *et al.* (1952), Brown (1958), and Pugh (1962).

D. The Community

In the foregoing discussions and examples, some references have been made to specific fungal communities. But the real biological communities in nature comprise not just fungi, but also other organisms: microbes, and higher plants and animals, form a coherent system with a considerable amount of interdependence and interaction. The constituents of the community have all been selected from a considerably wider pool of available organisms by environmental features of the habitat, and by antagonistic and symbiotic features emerging from their existence together. Fungi are not only recipients of such influences but may make important formative contributions to the habitat through improving soil structure and making available or storing nutrients and thus affecting soil fertility. They may also exert major selective influences on the more apparent organisms in the habitat, most obviously by causing disease. But there are other ways in which fungi affect apparently more dominant organisms in an area. Fairy rings affect the vegetation at their site, and not always in a minor way. Ramsbottom (1926) has described gorse and bramble being driven back by advancing rings of *Tricholoma gambosum*. Much work is still needed on community relationships involving fungi. Most of what we do know of synecology as well as of autecology of fungi is incomplete, and usually it is based on some stage in the life history that is of economic interest. This has been largely because funds are more readily available for such work. Some of the facts that should be known about a fungus in order to understand its autecology, its relationship with the factors in its environment, and its role in the community, include the range of suitable substrata, the stage of colonization of and activity in these, the modes of survival, and how all these are affected by altering the conditions in the environment. Autecology and synecology cannot at this level be maintained as separate departments of knowledge because both are elements in the relationship of fungi with their full environment.

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